

PLANT ECOLOGY OF THE BULLI DISTRICT.

PART I: STRATIGRAPHY, PHYSIOGRAPHY AND CLIMATE; GENERAL DISTRIBUTION
OF PLANT COMMUNITIES AND INTERPRETATION.

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(Plate xv.)

[Read 25th November, 1936.]

Introduction.

The area studied extends from Darke's Forest on the north to Towradgi Creek on the south, and from the coast up to seven miles inland (Plate xv). In this area, a wide range of rock types occurs, with consequent variation in soils; moreover, the unusual physiography leads to important results ecologically.

In this paper a general survey is made of the stratigraphy, the physiography and the climate of the area. The main plant communities are briefly mentioned, and interpretation of these as seres, subclimax, climax and postclimax vegetation is attempted. In subsequent papers each community will be dealt with in greater detail; the chief features of the soil types listed; and the comparison of leaf-size, and life-form spectra, undertaken.

The author acknowledges great indebtedness to Professor J. McLuckie, under whose guidance ecological observations of this area were commenced; and to Professor T. G. B. Osborn, for stimulating criticism.

Systematic names, except those to which the respective authors' names are appended, are those used in Moore and Betche (1893), or, for Pteridophytes, those used in the recent Check-List (Melvaine, 1936).

Stratigraphy and Physiography. (Plate xv.)

Except for small and unimportant dykes and sills, there are no igneous rocks in the district. Besides the recent soil (alluvial, or wind-blown sand), increasing in importance as the coastal plain widens, and the talus slopes below the scarp, which are considered as part of the rocks from which they are derived, the following is the sequence of sedimentary rocks:

| | | |
|-----------|---|-----------------------|
| | } | Wianamatta Shale. |
| Triassic: | | Hawkesbury Sandstone. |
| | | Chocolate Shale. |
| | | Narrabeen Sandstone. |
| Permian: | | Upper Coal Measures. |

The bedding of these strata appears at first sight to be almost horizontal, but actually there is a marked dip towards the north and west. It is to this dip that the unusual physiography can be attributed, the main features being the coastal plain, widening towards the south; the terraced slopes running back from the plain to the Hawkesbury Sandstone scarp; and above the scarp the flat plateau gently sloping north and west, dissected to some extent, especially towards the southern extremity of the area studied.

The widening of the coastal plain is caused by the greater amount of soft rock exposed below the Hawkesbury Sandstone as the strata rise to the south; this softer rock weathers, and the sandstone, left projecting, breaks off from time to time, the perpendicular face of the scarp being thus maintained. One such fall of rock occurred recently above the town of Thirroul, and cleared a wide swathe through the underlying brush vegetation of the slopes (Pl. xv, A).

The following figures are quoted from Griffith Taylor (1923):

| Distance from Sydney. | Locality. | Height of Upper Coal Measures. | Width of Plain. |
|--------------------------|--------------|-----------------------------------|-----------------|
| 33 miles | Otford | near sea level | nil |
| 44 miles | Bulli Pass | 300 feet | 2 miles |
| 55 miles | Mt. Kembla | 800 feet | 7 miles |
| 66 miles | Shellharbour | 1,000 feet | 12 miles |

Although these figures are at variance with Harper (1912) as to the position of junction of the Upper Coal Measures and the Narrabeen Series, they convey the reason of the occurrence and conformation of the coastal plain.

With the widening of the coastal plain, the conditions for vegetation immediately adjacent to the sea change. Whereas in the northern part of the district studied there are short beaches lacking sand-dune formations, interspersed with steep sea-cliffs carrying a typical vegetation, to the south the beaches are longer and the ground lying behind flatter, so that sand-dunes are frequent. In addition, the widening plain gives additional catchment for the easterly-flowing creeks, and alluvial soils become more important. These creeks, in the southern parts of the area, expand near the sea to subsaline lagoons, due apparently to the difficulty of access to the sea, a possible result of uplift. The vegetation bordering these lagoons is also typical.

Turning from the plain itself to the slopes running back to the vertical scarp, we find a considerable amount of terracing, the result of alternate bedding of hard and soft strata. This terracing is important from the aspect of brush development. The slopes are also dissected with gullies by creeks running down to the plain.

Coming to the plateau itself, we find the greater part of it consists of an undulating surface, for the most part with a deep, mature soil, and little exposed rock. The surface slopes north towards the Sydney geosyncline, and west towards the Nepean River, so that the streams of the plateau do not reach the coast directly. The whole of this sandstone plateau running north and west has been termed the "Nepean Ramp".

At Darke's Forest, on the north of the area studied, a small isolated cap of Wianamatta Shale occurs. To the south of the area, the westerly-flowing creeks running into Cataract River have, following pronounced post-Tertiary uplift, eaten through the Hawkesbury Sandstone, exposing the underlying Chocolate Shale and Narrabeen Sandstone. The dissected areas of the Hawkesbury Sandstone carry vegetation differing from that of the level parts of the plateau.

Climate.

The following figures are given for Wollongong, on the coast immediately to the south of the area studied:

| | Jan. | Feb. | Mar. | Apr. | May. | June. | July. | Aug. | Sept. | Oct. | Nov. | Dec. |
|--------------------|------|------|------|------|------|-------|-------|------|-------|------|------|------|
| Daily Temperature— | | | | | | | | | | | | |
| (°F.) Maximum* | 79·2 | 78·7 | 76·8 | 72·6 | 67·1 | 62·7 | 61·8 | 64·4 | 68·6 | 72·4 | 75·1 | 77·6 |
| Minimum* .. | 62·3 | 62·6 | 60·4 | 56·3 | 51·3 | 47·8 | 46·0 | 47·0 | 50·4 | 53·7 | 57·1 | 60·4 |
| Relative humidity | 75 | 76 | 76 | 76 | 75 | 76 | 75 | 71 | 68 | 69 | 69 | 73 |
| Rainfall (inches) | 4·41 | 4·61 | 4·65 | 5·32 | 4·59 | 4·22 | 3·96 | 2·29 | 2·61 | 2·71 | 2·68 | 3·60 |

Average Maximum Daily Temperature, 71·4° F.—Average Minimum Daily Temperature, 54·6° F.—Average Relative Humidity, 73%.—Total Yearly Rainfall (average), 45·65 inches.

The Meyer Ratio (P./s.d.) calculated from the above figures is just under 300, and mature soils throughout the district studied were typically podsolized.

The following figures for average total annual rainfall are given for other stations in or adjacent to the area: Sherbrooke, 58·63; Madden's Plains, 58·94; Appin, 36·04 inches.

(The first two stations are within the area studied, on the plateau at an elevation of about 1,200 feet, and within two miles of the scarp; the third is immediately to the north-west of the area studied, some twelve miles from the coast.)

It is apparent that the coastal climate is very similar to that of the Sydney district, but that, behind the coastal plain, the upper slopes and the plateau have a higher rainfall, due to the forcing upwards of moisture-laden air from the sea. Proceeding inland from the eastern edge of the plateau, however, the rainfall decreases rapidly.

The higher rainfall of the eastern edge of the plateau, coupled with the frequent occurrence of mists, produces climatic conditions sufficiently differing from those of the Sydney district to explain partly the greater prevalence of swamp or moor communities on the plateau, as at Madden's Plains.

The effect of winds on the vegetation of the area is important, especially from the two following aspects: (1) the physiographic shelter available from the winds from the general direction of the west (amongst which the south-westerly winds are especially important) is the primary factor conditioning the development of brush (or sub-tropical rain forest); (2) the sea-winds have an important effect on the vegetation near the coast. The effect of winds on dune-formation on the New South Wales coast has been dealt with by Andrews (1912), and need receive no further attention here. The sea-winds also have important effects on the sea-cliff vegetation from Austinmer northwards. Although not dry, they aid in inhibiting tree development, and in stunting many of the shrubs of the cliffs, while the spray carried by them tends to cause the development of halophytic types on the lower parts of the cliffs.

Under the heading of climate, the local low saturation-deficit that has been observed in certain situations may be briefly mentioned. In conditions of shelter, a microclimate of higher relative humidity occurs, which may be regarded partly

* Average for month.

as a result of physiographic shelter, and as such as a cause of the corresponding vegetation; but, especially at lower levels in the brush, it must be regarded as an effect of the vegetation in decreasing evaporation. In the extensive swamps of the plateau, in conditions of extreme exposure, the low but dense vegetation, by reducing wind effects, materially acts to retain a low saturation-deficit, near ground-level, and to maintain the swamps in their present state by reducing evaporation. This must be regarded as entirely a result of the vegetation, whereas in the microclimate of the brush, cause and effect are so intimately mingled as to be indistinguishable.

GENERAL DISTRIBUTION OF COMMUNITIES.

VEGETATION OF THE PLATEAU.

(1). *Hawkesbury Sandstone.*

This is subdivided as follows: (a) The *Eucalyptus Sieberiana* association, and variations; (b) Developments subject to physiographic shelter; (c) Lithoseres; (d) Extensive swamp or moor communities; (e) Vegetation of the Scarp.

(a). *Eucalyptus Sieberiana Association.*

This is the most extensive vegetation on mature soils of the Hawkesbury Sandstone. The association forms a low forest with a very marked shrub stratum. The association is similar to that found in the Sydney district, somewhat poorer floristically, and with few additional species. The main floristic features are given below.

Tree stratum.—Besides the dominant *Eucalyptus Sieberiana*, *E. corymbosa* occurs occasionally, especially in the drier situations, whilst *E. micrantha* Benth. is of occasional occurrence, especially approaching swamp conditions. The low-tree stratum is not pronounced, *Banksia serrata* being common but somewhat local.

Shrub stratum.—The great variety of sclerophyll shrubs is the most striking feature of the association. The following are especially abundant: *Banksia ericifolia*, *Acacia juniperina*, *A. suaveolens*, *Bossiaea heterophylla*, *B. scolopendria*, *Dampiera stricta*, *Dillwynia floribunda*, *Epacris microphylla*, *E. obtusifolia*, *Grevillea oleoides*, *Hakea pugioniformis*, *Isopogon anemonifolius*, *Lambertia formosa*, *Leptospermum scoparium*, *Leptomeria acida*, *Leucopogon juniperinus*, *Olar stricta*, *Persoonia lanceolata*, *P. salicina*, *Petrophila pulchella*, *Pimelea linifolia*, *Ricinocarpus pinifolius*, and *Sprengelia incarnata*.

Herbs.—*Xanthorrhoea hastilis*, *Gahnia psittacorum* and *Xerotes longifolia* are the most abundant large herbs; of the smaller herbs the following are especially important: *Haemodorum planifolium*, *Leptocarpus tenax*, *Lepyrodia scariosa*, *Patersonia glauca*, *Stackhousia viminea*, and *Xerotes flexifolia*. The most important climbing plant is *Cassytha pubescens*.

Variations.—The following variants within the association deserve notice:

(i). On the short gradual slope running down towards the scarp (as at B, Pl. xv), where excellent drainage renders the soil drier, but where protection from the west is greater than on most of the plateau, certain more mesophytic shrubs and herbs are mixed with the sclerophyll element. In particular, *Putenaea daphnoides*, *Olearia elliptica*, *Gleichenia flabellata*, *Lycopodium densum* and *Persoonia mollis* may be noted. Due to the drier soil conditions, the relative importance of *Eucalyptus corymbosa* increases slightly.

(ii). On the drier slopes running in a more or less westerly direction, especially approaching the western limit of the area, where the rainfall is less, the proportion of *E. corymbosa* to *E. Sieberiana* also rises, but with no marked change in the composition of the lower strata.

(b). Developments subject to Physiographic Shelter.

In regions of greater dissection, higher associations develop, the spatial sequence being *E. piperita* association, *E. pilularis* association, and brush. The effects are due primarily to the topography, and do not in any way represent an autogenic succession. The immediate causes are partly shelter from wind, but, more important, the higher humus content and water-retaining capacity of the soil, and a high moisture content not associated with poor drainage. The smaller prevalence of fires in these associations is a major cause in determining the high humus-content, as also is the higher water-content.

E. piperita is found on the upper slopes of the sides of gullies, especially near Loddon Falls (Pl. xv, C), and in situations between the two arms of Cataract Reservoir. *E. pilularis* is found on the lower slopes of gullies in the latter area (as at D, Pl. xv). Associated with both are the low trees *Exocarpus cupressiformis*, *Acacia longifolia* and *Persoonia linearis*, and the shrubs *Trachymene Billardieri*, *Leucopogon lanceolatus*, *Cassinia denticulata* and *Hakea saligna*, together with shrubs and herbs of the drier areas.

Brush only develops in situations of extreme shelter, as below the Loddon Falls. It is dealt with in a later section.

In other districts, *Angophora lanceolata* is found associated with *E. piperita* in situations such as the above. It has not been observed in this district, but immediately to the north, at Helensburgh, it occurs at the heads of Hawkesbury Sandstone gullies.

(c). Lithoseres.

Xeric lithoseres proceed on the few exposed rock surfaces of the plateau where a high water-table does not occur, the initiating stages being chiefly lichens, with a few mosses. Prominent among the first low shrubs are *Darwinia taxifolia* and *D. virgata*, and the numerous sclerophyll shrubs of the *E. Sieberiana* association follow. The fairly abundant areas interspersed amongst the *E. Sieberiana* association, where the soil is shallow and the highest development is a shrub community, are regarded as a stage in this succession.

More often, the colonization of bare rock proceeds through the intermediate local swamp sere, due to a high water-table, often caused by cupping of the underlying rock. Mosses constitute the first stage, followed by herbs, especially species of *Drosera*, *Utricularia lateriflora* and *Lepyrodia scariosa*, and similar types. This stage proceeds imperceptibly to a local swamp community, in which the following species are most abundant: *Banksia latifolia* var. *minor*, *Epacris microphylla*, *Hakea pugioniformis*, *Oxalis stricta*, and *Symphyoneme paludosa*; *Bauera rubioides*, *Chorizandra sphaerocephala*, *Gahnia psittacorum*, *Gleichenia dicarpa*, *Goodenia bellidifolia*, *Gymnoschoenus sphaerocephalus*, *Hypolaena lateriflora*, *Lepidosperma laterale*, *Leptocarpus tenax*, *Lepyrodia scariosa*, *Mitrasacme polymorpha*, *Restio complanatus*, *Selaginella uliginosa*, *Sprengelia incarnata*, *Xanthorrhoea hastilis*, and *X. minor*.

This community proceeds, by emphasis of the shrubs and decline of the sedges, until the *E. Sieberiana* association is reached, *E. micrantha* Benth. being prominent at the ecotone. This succession is characterized by a gradual lowering of the water-table.

(d). Extensive Swamp or Moor Communities.

Large areas of the sandstone are covered with a mixed sedge-swamp, in some cases with the addition of shrubs tolerant of swamp conditions. The factor

preventing development of a higher type of vegetation is the high average water-table. The low pH and high humus-content of the soil are secondary.

The topography where these communities occur is moderately flat, but with sufficient slope, at first sight, to cause wonder at the swamp conditions. Briefly, the apparent causes of the high water-table are: (1) Slowness of evaporation at ground-level, already mentioned. (2) An extremely clayey horizon at a depth of about 4 feet. (3) The tussocky nature of the plants, retarding water flow. (4) The presence of peculiar furrows, at intervals of one to two yards, at right angles to the normal slope and drainage. These, although not universal, are surprisingly frequent and regular; they may partly be due to the burrowing activities of the crayfish which are present in large numbers throughout these swamps.

In the large swamps near Sublime Point (as at Pl. xv, E) the following species are most important (in order of decreasing abundance):

Larger Herbs: *Gymnoschoenus sphaerocephalus*, *Lepidosperma Forsythii* Hamilton, *Lepyrodia scariosa*, *Chorizandra sphaerocephala*, *Restio complanatus* and *Xanthorrhoea minor*.

Smaller Herbs: *Selaginella uliginosa*, *Hypolaena lateriflora*, *Lycopodium laterale*, *Leptocarpus tenax*, *Goodenia bellidifolia*, *Xyris gracilis*, *Mitrasacme polymorpha* and *Epacris obtusifolia* (dwarfed).

Shrubs are very rare, being represented by scattered individuals of *Persoonia salicina*, *Hakea pugioniformis* and *Leptospermum juniperinum* Sm. In the somewhat drier community at Madden's Plains (as at Pl. xv, F), shrubs, especially the above species, together with *Banksia paludosa* and *Melaleuca squarrosa*, become more prominent, as also does *Xanthorrhoea minor*.

The ecotone between these communities and the *E. Sieberiana* association is similar to that bordering the local swamps mentioned in the preceding section. In several isolated instances, young specimens of *E. micrantha* Benth. extend beyond the tree limit, indicating a forward succession. In most cases, however, the limits are static, and swamp conditions cannot be superseded by a uniform increase in level due to plant remains. The soil is in most cases already very deep—in some cases more than sixteen feet, with plant remains occurring at a considerable depth. The water-table can only be lowered by allogenic causes, e.g., the working back of the Loddon Falls gorge by erosion, leading to better drainage conditions. The sequence of events which originally caused these swamps is obscure, but they have apparently been in their present state for a very long period.

(e). *Vegetation of the Scarp.*

Conditions on the face of the scarp and on the ledges and local small ravines which occur on it vary from very dry and exposed to moist and sheltered. Corresponding plants occur in these varying situations, and succession proceeds up to a certain stage, but trees are never formed on account of the transient nature of the surface and the frequent falls of rock.

Next to lichens, the mats of *Cyclophorus serpens*, *Polypodium Billardieri* and *Dendrobium linguiforme* are most important in colonizing dry rock faces. When sufficient soil is formed, the following types occur: *Actinotus Helianthi*, *Dracophyllum secundum*, *Epacris coriacea*, *E. longiflora*, *Xanthorrhoea arborea* and *Xanthosia pilosa*.

In moister situations, mosses and liverworts initiate the sere, which develops up to a stage where *Blechnum Patersoni*, *B. capense*, *Gleichenia circinata* and *Hypolaena lateriflora* and bushes of *Callicoma serratifolia*, *Cassinia denticulata*, *Doryphora sassafras*, *Pultenaea daphnoides* and *Tristania laurina* are prominent.

(2). *Wianamatta Shale.*

As one passes from Hawkesbury Sandstone to Wianamatta Shale at Darke's Forest, there is a pronounced change from *Eucalyptus Sieberiana* low forest to a high forest dominated by *E. piperita* and *Angophora lanceolata*. The low-tree stratum is much more pronounced than on the sandstone, *Acacia binervata*, *A. longifolia*, *A. rubida* and *Exocarpus cupressiformis* being the important species. In the shrub layer, the more mesophytic element is represented by *Hakea saligna*, *Leucopogon lanceolatus*, *Olearia ramulosa*, and *Persoonia ferruginea*, and, more rarely, *Cassinia aurea*, *Lomatia ilicifolia*, and *Olearia viscidula*. In addition there is an admixture of typical sandstone forms, *Acacia myrtifolia*, *Banksia ericifolia*, *B. spinulosa*, and *Persoonia salicina* being most important.

The most important herbs are *Blechnum cartilagineum*, *Haloragis teucroides*, *Pteridium aquilinum* and *Viola hederacea*, with such typical sandstone species as *Doryanthes excelsa* and *Xerotes longifolia*.

The change of vegetation as one passes from sandstone to shale must be attributed to the greater water-retaining capacity of the soil derived from the latter. The absence of certain trees (notably *Syncarpia laurifolia*) characteristic on Wianamatta Shale elsewhere is surprising, and appears to be due to isolation rather than unsuitability of habitat.

(3). *Narrabeen Series.*

The vegetation of the Chocolate Shale and Narrabeen Sandstone exposed by the dissection of the plateau is discussed in this section; that on these rocks on the coastal slopes is discussed later.

Except in shelter, the vegetation on soils derived from both the above rock types is high *Eucalyptus* forest, dominated in the former case by *E. saligna*, and in the latter by *E. piperita*. Important constituents of the low-tree stratum in both communities are *Acacia longifolia*, *A. mollissima*, and *Exocarpus cupressiformis*, and of the shrub stratum *Indigofera australis*, *Persoonia ferruginea*, *P. lanceolata*, *P. salicina*, *Pimelea ligustrina*, *Pomaderris elliptica* and *Prostanthera Sieberi* Benth. The most abundant herbs are *Blechnum cartilagineum*, *Imperata arundinacea*, *Pteridium aquilinum* and *Viola hederacea*.

In conditions of partial shelter on the Chocolate Shale and efficient shelter on the Narrabeen Sandstone, brush develops. The constitution of the brush is discussed later. On Narrabeen Sandstone, in partial shelter, the *E. saligna* association forms. Brush elements, especially *Livistona australis* and *Alsophila australis*, are frequently scattered amongst the *E. piperita* and *E. saligna* associations in conditions where there is insufficient shelter for true brush to occur.

Surrounding the Cataract Reservoir, an interesting zonation occurs due to constant raising of the water-level (as at Pl. xv, G). Following the aquatic stages, there is an area of mud, frequently exposed, and inhabited only by introduced annuals; above this, a narrow zone of several species of *Juncus*, leading back through grasses (chiefly *Poa annua* (introd.) and *Imperata arundinacea*) to a shrub zone dominated by *Leptospermum flavescens* and *Melaleuca squamea*, and thence to the *Eucalyptus* forest.

VEGETATION OF THE SLOPES AND COASTAL PLAIN.

This section is subdivided as follows: (1) *E. pilularis* association and variant; (2) Brush; (3) Sand-dune succession; (4) Subsaline lagoon succession; (5) Sea-cliff vegetation. The vegetation altered by clearing and grazing has been omitted in the present study.

(1). *E. pilularis Association and Variant.*

Except where there is sufficient shelter and soil moisture for the development of brush, the coastal slopes and plain support a high forest dominated by *Eucalyptus pilularis*, with *E. paniculata* and *Syncarpia laurifolia* fairly commonly represented. The soil is derived chiefly from Narrabeen Sandstone and from the varied strata of the Upper Coal Measures (ranging from shale to coarse sandstone), but is also influenced by the rock lying above. Other smaller trees prominent in this association are *Casuarina torulosa*, *Notolea longifolia* and *Persoonia linearis*, and, especially in the moister situations, *Acacia binervata*. Other important elements are *Acacia myrtifolia*, *A. suaveolens*, *Helichrysum bracteatum*, *H. diosmifolium*, *Hibbertia dentata*, *Indigofera australis*, *Leucopogon lanceolatus*, *Oryzobium trilobatum*, *Persoonia salicina*, *Pimelea ligustrina*, *Prostanthera Sieberi* Benth., *Senecio dryadens* and *Zieria Smithii*, and the herbs *Hypochaeris glabra* (introd.), *Pteridium aquilinum*, and more rarely *Imperata arundinacea*, *Doodia aspera* and *Xerotes longifolia*. The introduced *Rubus fruticosus* is also abundant.

In soils derived from a tuffaceous mudstone in the Towradgi area, a mixed Eucalyptus forest occurs, of which the most important species are *E. botryoides*, *E. eugeniioides*, *E. longifolia*, *E. paniculata* and *E. punctata*. The lower strata are similar to those of the climax of the subsaline lagoon succession discussed later.

(2). *Brush.*

East of the scarp, brush occurs on the uppermost slopes (except at the most prominent ridges) (e.g., Pl. xv, H), and on the inner side of terraces and in gullies at a lower level. These situations are sheltered from dry winds, and provided with copious water-supply, and conditions are favourable for the development of soil humus. The scarp, besides offering shelter from dry winds, decreases insolation by cutting off direct sunlight shortly after noon.

Brush also develops in partial shelter from the west on soils derived from the Chocolate Shale (e.g., Pl. xv, J), and under more extreme conditions of shelter on soils derived from Narrabeen and Hawkesbury Sandstone. In all cases, the ecotone between the brush and the adjacent Eucalyptus forest is indistinct, numerous brush types extending beyond the limit of the true highly-integrated brush formation.

Except for occasional high trees of *Eucalyptus saligna* and *Ficus rubiginosa*, the coastal brush is composed of a great number of species of trees of moderate height, mostly of the laurel-leaved type. The following are of particular importance:

Cargillia australis R.Br., *Ceratopetalum apetalum*, *Doryphora sassafras*, *Ficus stephanocarpa* Warb., *Eugenia Smithii*, *Hedycarya Cunninghamii*, *Laportea gigas*, *Livistona australis*, *Omolanthus populifolius*, *Panax sambucifolius*, *Pittosporum undulatum* and *Sloanea australis*. Of these, *Livistona australis* is singled out as the most abundant and characteristic species.

In the brush, low trees are rare, the tree-fern *Alsophila australis* being the sole exception; but on the ecotone between brush and Eucalypt forest, *Breynia oblongifolia*, *Eupomatia laurina*, *Lantana camara* (introd.), *Rhodamnia trinervia* and *Synoum glandulosum* are abundant.

Of the ground layer, the ferns *Adiantum acthiopicum*, *A. formosum*, *Asplenium flabellifolium*, *Histiopteris incisa*, *Pellaea falcata* and *Pteris umbrosa*, and the herbs *Gymnostachys anceps* and *Pollia cyanococca*, are the most important members.

In addition, climbers and epiphytes form a distinctive portion of the brush, the most abundant being *Eustrephus Brownii*, *Lyonsia straminea*, *Palmeria scandens*, *Sarcopetalum Harveyanum*, *Senecio mikanioides* Otto (introd.), *Smilax australis* and *Stephania hernandifolia*; *Pleopeltis diversifolia*, *Davallia pyxidata* and *Asplenium nidus*.

It is certain that the brush was far more extensive in this region in former times, but the effect of settlement, and the ravages of fire, have had disastrous effects on an association only able to regenerate itself slowly after fire or partial clearing.

Inland, brush developed on soils derived from the Narrabeen Series is comparable to the coastal brush, but poorer floristically and less highly integrated. The brush occurring in extreme shelter on Hawkesbury Sandstone is very poor floristically, the only common trees being *Callicoma serratifolia*, *Ceratopetalum apetalum*, *Doryphora sassafras*, and *Tristania laurina*.

(3). Sand-dune Succession.

Succession from wind-blown dunes is proved to be acting in a forward direction in parts of the area, as at Towradgi, by examination of the soil underlying the seral communities behind the dunes. It does not, however, reach the climax, for in all cases the highest development on what has been sand-dune—*Eucalyptus botryoides*–*Banksia integrifolia* associates—meets the opposing succession from the subsaline lagoon (the *E. robusta* associates) (as at Pl. xv, K). Areas where a climax may have been reached in the past have been cleared completely.

The sere is normal, being represented thus: (1) *Festuca litoralis*–*Spinifex hirsutus*–*Carex pumila* associates. (2) Shrub-dune dominated by *Leptospermum laevigatum*, *Leucopogon Richei* and *Acacia Sophorae*. (3) *Eucalyptus botryoides*–*Banksia integrifolia* associates, with a shrub layer mainly composed of relics of the earlier stage.

(4). Subsaline Lagoon Succession.

The sere leading from the subsaline lagoons can be listed as follows: (1) *Phragmites communis* associates (a narrow belt in shallow water). (2) *Juncus maritimus* associates (a broad belt at the edge of the lagoon, subject to constant flooding). (3) Where the lagoon border is very flat, a small zone, the *Cladium junceum* associates. (4) *Casuarina glauca* associates, forming a low forest, the ground layers mainly composed of *Juncus maritimus*. (5) *Eucalyptus robusta* associates, with ground layers composed of members of the preceding seres, and *Gahnia psittacorum*. (6) Climax mixed forest in which *Eucalyptus botryoides*, *E. eugenioides* and *E. paniculata* are predominant. The lower strata contain elements of the former stages of this succession and of the hind-dune vegetation (e.g., *Cladium junceum*, *Gahnia psittacorum*, *Leucopogon Richei*, *Leptospermum laevigatum*), with a definite brush element (e.g., *Breynia oblongifolia*, *Clerodendron tomentosum* and *Stephania hernandifolia*).

(5). Sea-cliff Vegetation.

Vegetation on the steep sea-cliffs, as at Austinmer (Pl. xv, L), is subjected to great exposure to sea-winds, and, on the lower portions, a high concentration of salt. These factors, coupled with frequent landslips, prevent the development of anything higher than a shrub community. An interesting zonation occurs, but does not constitute a true case of succession:

(1) A zone of halophytic herbs, the most prominent being *Lobelia anceps* and *Samolus repens*, and less commonly *Apium prostratum*, *Plantago varia* and *Scaevola hispida*. This merges into:

(2) A shrub zone, dominated by *Banksia integrifolia*, *Leptospermum laevigatum*, *Westringia rosmariniformis*, and small shrubs of *Casuarina glauca*.

Behind this zone the vegetation passes with an indefinite ecotone to the *Eucalyptus pilularis* association, with trees of *Banksia integrifolia*, decreasing in number with distance from the sea.

Interpretation.

Omitting communities which are either seres or are held in a condition obviously below the climax and are unable to proceed by a forward autogenic succession to the climax, we may summarize the distribution of the main communities as in the following table:

| Conditions of Shelter. | Parent Rock of Soil (coarsest soil to the left). | | | | |
|-------------------------------|--|---|---|--|--------------------------------|
| | Hawkesbury Sandstone. | Narrabeen Sandstone. | Wianamatta Shale. | Upper Coal Measures. | Chocolate Shale. |
| Flat or undulating conditions | <i>E. Sieberiana</i> association. | <i>E. piperita</i> association. | <i>E. piperita</i> - <i>Angophora lanceolata</i> association. | <i>E. pilularis</i> association; mixed <i>Eucalyptus</i> forest (tuffaceous mudstone.) | <i>E. saligna</i> association. |
| Moderate shelter | <i>E. piperita</i> association. | <i>E. saligna</i> association (inland); <i>E. pilularis</i> association (coastal slopes). | Conditions do not occur. | Brush (low grade). | Brush. |
| Good shelter .. | <i>E. pilularis</i> association. | Brush (low grade). | Conditions do not occur. | Brush. | Brush. |
| Extreme shelter | Brush (low grade). | Brush. | Conditions do not occur. | Brush. | Brush. |

From this table it will at once be seen that a prominent part is played, in the distribution of communities in this area, by the influence of parent rock on vegetation by the medium of the derived soil. The influence of topographic shelter can likewise be gauged.

Although no definite objective test can be made as to what constitutes the climax association, and such interpretations must necessarily be guided by personal opinions, the following classification is submitted:

The climax formation for the district is *Eucalyptus* forest (sclerophyll forest). Brush in all cases constitutes a physiographic postclimax. Weaver and Clements (1929) give the following details concerning the postclimax (p. 78): "Local communities may develop or persist where especially favourable conditions of

soil, humidity, etc., exist, which represent a more highly developed stage than the present climatic climax of the region." Subsequent statements by Clements (1936, p. 269) do not appear to alter this interpretation, although the relict nature of the postclimax is emphasized.

It seems logical to extend the concept of the postclimax, within the major limits of the formation, to the smaller units of associations. Thus the climax is taken as the highest association that develops in homologous positions, on mature soils with undulating to flat topographical conditions, on the soils derived from the varying rock types; the climax association thus varying with the parent rock, and an association which is the climax on one soil corresponding to a post-climax development on a soil of coarser texture. Thus the following climaxes are recognized:

- Hawkesbury Sandstone: *Eucalyptus Sieberiana* association.
- Narrabeen Sandstone: *E. piperita* association.
- Wianamatta Shale: *E. piperita*-*Angophora lanceolata* association.*
- Upper Coal Measures (mostly): *E. pilularis* association.
- Upper Coal Measures (tuffaceous mudstone): Mixed *Eucalyptus* forest.
- Climax of sere from Subsaline lagoon: Mixed *Eucalyptus* forest.
- Chocolate Shale: *E. saligna* association.

Comparing the communities listed in the table for Hawkesbury Sandstone, Narrabeen Sandstone, and Upper Coal Measures, we see that if similar associations in the respective columns be joined, the lines represent diagonals. On mature soils on the coastal plain derived from shales of the Upper Coal Measures, the *E. pilularis* association forms the climax; on soils from this parent rock, brush forms as a postclimax, in varying degrees of integration depending on varying degrees of shelter. If we take a homologous situation on soil derived from Narrabeen Sandstone to that on which the *E. pilularis* association develops on the coastal plain, the vegetation is found to be the *E. piperita* association. In conditions of greater shelter, the *E. pilularis* association (or, inland, the corresponding *E. saligna* association) develops; in any greater shelter, brush develops. These are regarded as primary and secondary postclimaxes. On mature soil derived from Hawkesbury Sandstone, with undulating topography, the highest community found in this district is the *E. Sieberiana* association; primary, secondary and tertiary postclimaxes on soil from this rock are represented by the *E. piperita* association, the *E. pilularis* association and low-grade brush; the first in partial, the second in good, the last only in extreme shelter.

Turning now to communities below the climax, we can dismiss the following as being legitimate cases of autogenic succession leading to the climax of the region:

- (1) Xeric lithoseres as on Hawkesbury Sandstone leading eventually to the *E. Sieberiana* association or corresponding climax.
- (2) Lithoseres subject to moister conditions, as detailed under the Hawkesbury Sandstone vegetation, where local swamps form an intermediate stage.
- (3) The sand-dune sere (not observed to reach a climax in this district, but this negative observation is probably due to clearing).
- (4) The seres bordering the subsaline lagoons (*Phragmites communis* associes-*Juncus maritimus* associes-*Casuarina glauca* associes-*Eucalyptus robusta* associes), leading to climax mixed *Eucalyptus* forest.

* As stated earlier, it is probable that a climax richer floristically would develop if it were not for isolation.

Both (3) and (4) are subject to retrogression also in certain places, as by "blow-outs" caused by southerly winds in (3), and scouring in (4). Moreover, where a narrow belt of land occurs between dune and lagoon, (3) proceeds to *Eucalyptus botryoides*-*Banksia integrifolia* associates, (4) proceeds to *E. robusta* associates, and the seres meet at this point, the climax not forming (Pl. xv, K).

The remaining communities below the climax are regarded as subclimax vegetation in the restricted sense of Godwin (1929). The extensive swamps or moors of the sandstone plateau appear unable to proceed (except in the very few instances noted, insignificant from the point of view of total area), beyond the present state, except by allogenic causes, for reasons of high water-table. The varying vegetation of the sandstone scarp, proceeding by autogenic succession from the bare rock faces left by rock falls up to a certain stage, can never attain climax status under the present system of erosion, but can proceed to varying stages in the lithosere succession before the next fall brings the conditions back to the bare rock face stage again. The vegetation surrounding Cataract Dam represents a true subclimax due to periodic artificial raising of the water-table.

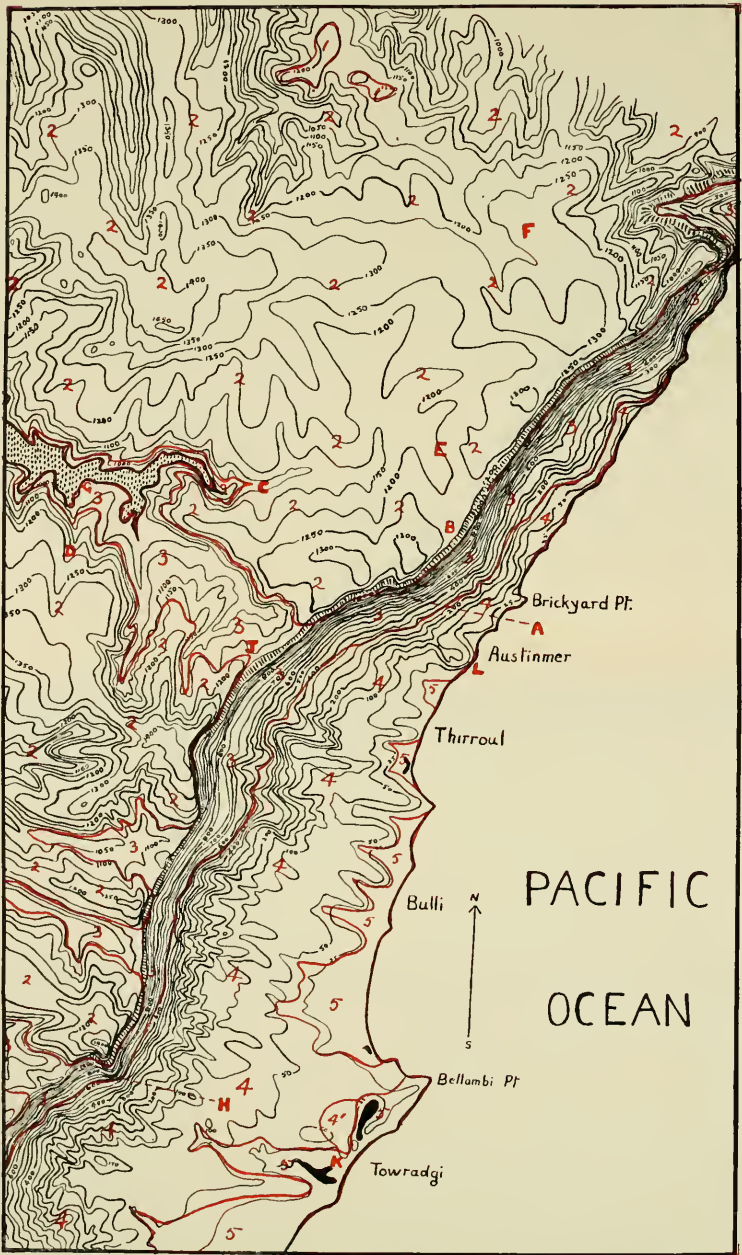
The sea-cliff vegetation, although it shows a clear zonation from the base of the cliff to climax forest on the cliff-top, does not represent a forward succession in time. Erosion causes inhibition of development, as on the sandstone scarp, and the actual result to the vegetation, due to this allogenic cause, is retrograde. Under the present conditions, corresponding portions of the cliff will always regenerate, following landslips, to their former vegetation, but no higher; and as a result of the erosion the cliff-face as a whole works backwards, to cause the destruction of the adjacent parts of the higher communities.

It will be gathered from the above that subclimax vegetation is a very important feature of the area. Indeed, cases of forward autogenic plant succession to the climax are believed to be far rarer in this country than is sometimes supposed, and a mere spatial zonation must always be examined very critically before it can be pronounced to represent a true succession.

The above interpretations may be regarded as unconventional, but it is submitted that, since the explanation of the basic causes of the distribution of communities has been suggested, the nomenclature of these communities is a secondary consideration. The terminology used in interpreting plant communities has become so involved that there appears to be a tendency to consider it an end in itself, and not a utilitarian method of classifying facts due to direct natural causes, the understanding of which is, in the end, the main object. The following remarks of Benjamin Moore epitomize well the necessary attitude in controversies of nomenclature: "Care is needed that in entering into disputations . . . terminology is not becoming confused so that the dispute is only over terms, instead of over things."

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Topographical and Contour Map of the Bulli District (1 inch = 1 mile; contour interval, 50 feet).